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SOME OBSERVATIONS ON THE DEVELOPMENT OF THE TESTICLE

BY

JAMES FOULIS, M.D., F.R.C.P.Ed.

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In order to trace out in a successful and satisfactory manner the various steps in the development of the testicle, it is necessary to be acquainted with the main facts in the development of the ovary, as the study of the development and growth of these two organs becomes more interesting and important, just in proportion as the homologies between them are laid bare in the various stages of their development.

Thus at once arises the question, is the ovary a tubular structure in the same sense that the testicle is? Then, too, as regards the theory of spermatogenesis, are the spermatozoa derived from the nuclei of cells, just as are the germinal vesicles of the ova? and are the cells which give origin to the spermatozoa in the male, and to the germinal vesicles in the ova, both derived from the germ epithelial cells in the early embryonic

condition? These and many other interesting questions at once arise as we study side by side the development of the testicle, and the development of the ova and the ovary.

Since the observations of Pflüger and Waldeyer on the development of the ova and the ovary were published, all observers are agreed that the first trace of the ova is among the germ epithelial cells, and that the germinal vesicles of the ova are derived from the nuclei of the germ epithelial cells; but all are not agreed as to the manner in which these germ cells become enclosed in the meshes of the ovarian stroma. Pflüger described the germ epithelial cells as growing downwards into the mesoblastic stroma in the form of columns of epithelial cells which enclose among them some of the primordial ova. These columns are the "egg tubes" of Pflüger. These "egg tubes" become broken up into rounded groups or "cell nests" by the continued in-growth of the stroma, and one or more cells in each group becomes a primordial ovum, the other cells remaining small to form the epithelial lining of the young Graafian follicles thus formed. According to this view, the ova and the cells lining the Graafian follicles are both derived from germ epithelial cells on the surface of the young ovary which grow downwards in the form of tubular columns into the subjacent vascular stroma. This view makes out that the young ovary is a tubular structure at an early stage of its development, just as the testicle is, and that the epithelial lining of the primitive tubules, and of the subsequent Graafian follicles, is from germ epithelial cells which do not develop into ova. Other observers hold that the germ epithelial cells do not grow downwards into the ovarian stroma in the form of tubes, "the egg tubes" of Pflüger, but that from the very first trace of the ovary, the vascular stroma grows outwards, and sends its young processes among the germ cells enclosing them in its meshes in groups of various sizes, and that the Graafian follicles are formed by the stroma enclosing one or more primordial ova, along with a number of smaller germ cells, which become the epithelial cells lining the young Graafian follicles.

Another view is that published by myself more than twenty-five years ago in my graduation thesis "On the Development of the Ova and the structure of the Ovary in Man and other

Mammalia." My conclusions were that the ova are derived from the germ epithelial cells, and that the nuclei of such cells become the large germinal vesicles of the ova, and that from the very first trace of a thickened germ epithelial layer on the surface of the young ovary, the young vascular stroma sends its processes outwards among these cells enclosing variously-sized and variously-shaped groups of them in its meshes, and that it is by the continued onward and outward growth of this stroma among the individual cells in each group that the Graafian follicles are formed. According to my view, all the included germ cells may become ova. By the growth of the vascular stroma not only round the groups of cell nests, but between and around the individual cells in the nests, the whole ovary at last becomes a mass of young ova enclosed in the meshes of the stroma, and at last each germ cell is enclosed in a single mesh of stroma, this last mesh becoming the young Graafian follicle. But, further, in accordance with this view, the cells lining the young Graafian follicles are derived from the cells of the vascular stroma, for I discovered that, even among the germ epithelial cells on the surface of the ovary, whenever a primordial ovum is seen it is found to be enclosed in a mesh of ovarian stroma. In all parts of such a young ovary each primordial ovum is found to have round its protoplasm a mesh of stroma; and so invariably is this the case, that I was forced to the conclusion that this capsule of young vascular stroma is the direct exciting cause of growth and development of each primordial ovum, and that nutriment is conveyed to such growing ova by the cells in the vascular stroma itself. Here, then, we have the conclusion that while all the ova are derived from germ epithelial cells, and that the Graafian follicles are formed by the ultimate meshes of the vascular stroma around the ova, the cells lining the Graafian follicles are derived from the stroma, and not from the germ epithelial cells, as was described by Pflüger, Waldeyer, and other observers; and as regards the theory of the tubular structure of the ovary, I came to the conclusion that the so-called tubes are only microscopic appearances seen in sections of variously-sized and variously-shaped groups of included cell nests. Since these conclusions were published, although I have followed pretty closely the recent literature on the sub-

ject, I have seen and read nothing to cause me to alter my views in any way.

Whether the "egg-tubes" of Pflüger do or do not take part in the formation of the Graafian follicles, it is certain that in the ovaries of a child at birth, there are not less than 70,000 included ova: but how few of these come to maturity!

It is interesting to observe that in all mammals the ovum can only escape from a ripe Graafian follicle by bursting through the wall of the follicle, and that it would at once fall into the peritoneal cavity were it not for the fimbriated extremity of the Fallopian tube which catches it and conveys it into the cavity of the uterus.

While not allowing that the ovary is a tubular structure in the sense in which Pflüger described it, there can be no doubt that the testicle is from the first stages of its existence a tubular structure, and that its seminal secretion with its living spermatozoa is produced within its tubes, and that this secretion can only escape from the organ by the vas deferens, a very long tube, derived from the Wolffian duct, which in the embryo is connected at its lower end with the cloaca.

While it is thus clear that the ova are derived from the germ epithelial cells, and that the Graafian follicles are the ultimate meshes in the ovarian stroma and lined with cells derived either from the germ epithelial layer or from the cells in the stroma, it is by no means clear how the tubes of the testicle are formed, and from whence are derived the cells lining those tubules from which are produced the living spermatozoa.

The subjects of ovulation and spermatogenesis can only be cleared up by knowledge of the minute structure both of the ovary and testicle, and this can only be acquired by tracing out the development of these organs from their earliest appearances in the embryo; and even then we have not begun at the beginning of the study, for it is absolutely necessary to trace back to their origin from the three primitive germinal layers all those structures which play so important a part in the later development of the organs. Is the germ epithelium, for instance, derived from the epiblast or from the mesoblast or from the hypoblast? Are the Müllerian ducts and the Wolffian ducts lined by cells derived from the epi-

blastic germinal layer? If the epithelium lining the Graafian follicles and the tubules of the testicle can only be produced from epithelial cells, it is most interesting to find out if the parent cells are of epiblastic origin. Much has been done by Kölliker and later observers to show that the Wolffian duct is derived from the epiblastic germinal layer, and according to Balfour and others the Müllerian ducts also have an epiblastic origin. These are points, however, which I only touch upon in passing as being of the greatest interest. My own investigations start from the already formed germ epithelium and from the already formed Müllerian and Wolffian ducts, all of which it is possible to see in the fresh and microscopic preparations in my possession.

The question of the origin of the tubules of the testicle and as to the origin of the cells lining those tubules is of the greatest interest. In the last edition of Quain's "Anatomy," vol. i. part i., Embryology, at page 126, there is a drawing representing a section of the germinal epithelium and adjacent stroma in a male chick embryo, taken from Semon, in which it is attempted to show that strands of cells growing up from the Wolffian body towards the germ epithelial layer, come in contact with enlarged primordial ova and cell nests, and that from these cell nests and primordial ova the epithelial cells lining the tubules of the testicle are formed, although all stages of the process have not been observed. If this origin of the cells lining the tubuli seminiferi should turn out to be correct, then, of course, there is established a most interesting homology between the germinal vesicles of the ova and the nuclei of the cells lining the tubuli seminiferi; for it is from these nuclei that the heads of the spermatozoa are supposed to be produced.

There certainly is a stage of development in the testicle, as is the case with the young ovary, when the whole gland seems to consist of a thick layer of epithelial cells capping a little outgrowth of stroma from the Wolffian body. It is at this stage that is impossible to say if the gland is male or female. In the case of the testicle, if there is at any time a connection between the germ epithelial cells and tubular outgrowths from the Wolffian body, it must be before the strong fibrous capsule ortunica albuginea of the testicle is formed, for this structure entirely shuts off the tubules from the outside world. Anterior

to the formation of this capsule there may be some connection between germ epithelial cells and tubules from the Wolffian body, but I know of no drawing which proves this, and I have not seen anything of the kind, though both in the young ovary and testicle it is possible to see certain tubular structures entering these glands at their base. In the testicle, as I shall presently show, this growth of tubules goes on until the whole capsule of the testicle is distended with tubules, which, according to my investigations, grow outwards from the Wolffian body, and do not at any time grow downwards from the germ epithelial layer. In the case of the young ovary, though tubules from the Wolffian body enter at the hilum and grow to a certain distance, they gradually abort, and take no part in the structure of the ovary itself.

My present researches were undertaken with the object of tracing out the origin of the tubuli seminiferi, and, if possible, of the cells lining them, from which are produced the spermatozoa. There is something very fascinating in the study of the development of the ova and of the spermatozoa; but this latter cannot be successfully done without first of all discovering the origin and source of the tubuli seminiferi.

Knowing that the vas deferens in the adult is represented in the embryo and fœtus by the Wolffian duct, it was necessary, in the first place, to find out the exact position of the Wolffian duct in its relation to the testicle in its earliest stages of development; but this was a difficult matter, because in glands so young it is not possible to say if we are dealing with the male or female organ.

Two or three years ago I discovered that the embryos of deer show the Wolffian bodies in a remarkably clear manner, and so I secured a number of them at different ages, and having prepared them, it was possible to study the Wolffian bodies both in fresh preparations and subsequently in microscopic sections. In an embryo of a deer, less than an inch in length when fully pinned out, it is possible to clear away the liver, and thus expose the Wolffian bodies. In such a young embryo the yolk-sac is still attached to the primitive intestinal tube, and the anterior and posterior limbs stand out as spade-like buds. The two Wolffian bodies may thus be seen like two long thick sausages, lying side by side on either side of the central mesentery and intestinal tube, and extending from the

site of the anterior limbs backwards to the pelvic region of the young animal, where, even at this early age, the two Müllerian ducts can be seen joining each other in the middle line (Plate vi. Fig. 12). The Wolffian bodies thus appear as two large reddish-brown sausage-shaped bodies, tapering off slightly at their ends. Under the microscope a white streak-like ridge, E, can be seen on the inner side of each Woffian body, almost in contact with the central mesentery, and extending up and down the Wolffian body for fully three-quarters of the length of each body. This white streak is the primitive germinal ridge, and in connection with this at its upper part both the ovary and testicle make their first appearance. I would particularly call attention to the upper end of this germinal ridge. In its connection with the Wolffian body it does not end abruptly, but seems to enlarge slightly, and then fade off into the substance of the Wolffian body.

It is important to notice this part, for it is here that we have the first appearance of the young testicle as a distinct body. There is here always an important connection between the young testicle and the Wolffian body. At its lower end the germinal ridge gradually fades off, and is in direct connection with the peritoneum which covers the lower end of the Wolffian body and other organs in the pelvic region. The germinal ridge may be looked upon as a fold of thickened peritoneum projecting out from the peritoneum covering the Wolffian body on its inner aspect, and at the lower end of the germinal ridge this peritoneum is in continuation with the general peritoneal layer which covers all the pelvic organs and parts in that region.

Turning now to Plate vi. Fig. 12, the two Wolffian bodies D D are well seen, and the germinal ridges E E are seen as described; and in Fig. 13, which is a more highly magnified drawing of one of the Wolffian bodies, the germinal ridge E may be seen enlarged at its upper end, and gradually fading off into the substance of the Wolffian body at its upper part B. The letter C points to the Müllerian duct.

In transverse sections the Wolffian bodies present the appearance as seen in Fig. 14, which is from a microphotograph of a section through the body of such an embryo as is depicted in Fig. 12.

In such a section the neural canal A is seen, and at F the

chorda dorsalis is clearly observed, while the letter M points to the aorta, full of blood corpuscles. The two Wolffian bodies D D are seen on each side of the aorta ; and it is interesting to note that the glomeruli occupy a situation in front and to the side of the aorta, from which they receive their blood supply, while the tubular parts of the Wolffian bodies lie to the outside of the aorta behind the situation of the glomeruli. The letter C points to the Müllerian duct in each Wolffian body. I would here like to call attention to the fact that in several of my preparations the lumen of the Müllerian duct can be seen in direct connection with the lumen of some of the tubes in the Wolffian body. In other words, my preparations show that in such an embryo the Müllerian duct is not a simple tube, but receives tubules from the Wolffian body. This observation may be of some importance in connection with the origin of the epithelium lining the Müllerian duct from the epiblast.

In Fig. 14 the young germ glands, ovaries or testicles are indicated by the letters B B on each side of the central mesentery G ; while the glomeruli receiving branches of blood supply from the aorta M are indicated by the letters E E.

So much then for the early appearance of the Wolffian bodies as seen in such a young embryo. These drawings have been most faithfully made, and correctly represent the appearances seen in such a young deer embryo.

Bearing these appearances in mind, let us look more closely at the young germ glands. They appear to the naked eye as two almost semicircular outgrowths from the Wolffian bodies on their inner side, B B, and project towards the mesentery in the middle line.

Under high powers of the microscope the young gland is seen to be a growth of stroma from the Wolffian body, capped over with a thick layer of epithelial cells, which are directly continuous with the peritoneal cells on its margins. Numerous blood-vessels, filled with nucleated embryonic blood corpuscles, can be seen in it, going up as far as the layer of epithelial cells on its surface ; but it is at this stage impossible to say if such a gland is an ovary or testicle.

But there is a stage in the development of the genital glands at which it is possible to distinguish between the ovary and testicle. As soon as the young gland becomes distinctly globular the difficulty is at an end. For by means

of a sharp razor it is now easy to slice off a minute piece of the gland in question ; and if such a piece is torn to shreds in a little water by means of needles, and then examined under the microscope, if it is an ovary the sliced-off piece will be found to consist of cells of various sizes, permeated in all directions by very vascular stroma, but without the slightest appearance of an enclosing fibrous capsule. If the gland in question is a testicle, there will always be found some trace of an enclosing peritoneal capsule. The testicle at this stage is always firmly attached to the Wolffian body at its upper part ; and if such a gland is sliced in half, that half which is still attached to the Wolffian body, may be placed under water and cleared out of its contents by means of fine needles ; and there remains a beautiful fibrous capsule. It is impossible to treat the half of an ovary in this way, as the organ, being very brittle and cellular, cannot be so dissected, and it has no fibrous peritoneal capsule, as is the case with the testicle.

It was while treating young ovaries and testicles in this way in my efforts to determine which was which that I made the following observation.

The delicate little capsule, which in the case of the testicle always remained after its contents were cleaned out, was found to be firmly attached by a stalk-like process of peritoneum to the peritoneal covering of the Wolffian body. Invariably I found a minute hole in the capsule thus left, and this hole had a distinct relation to the stalk of peritoneum attaching the testicle to the Wolffian body. Into this hole I could pass a small bristle, which, if pushed on, would go through the centre of the stalk connecting the capsule of the testicle to the Wolffian body.

If you now look at Plate ii. Fig. 4 the letters B B point to minute holes in the capsules of the two testicles which have been sliced in half and cleaned of their contents. This Fig. 4 represents the appearance seen on looking into the body of a fœtal deer, not more than two inches in length, after it had been prepared in such a way as to show the two Wolffian bodies D D. In the sliced capsules of the young testicles, the letters B B point to the minute holes in the capsules, as seen from the inside view. This hole is always seen in exactly this same situation in such young capsules, and as it is always present it must be of some

importance. A full description of this figure is given in the proper place; but what I have indicated suffices to show that the young testicle at this early age always possesses a firm fibrous capsule, which if cleaned out will always show in the same position as indicated in the drawing a minute hole through which some structures must pass from the Wolffian body into the capsule of the testicle. No other hole can be discovered in the whole capsule of the testicle; and it would appear that the entire tubular contents of the testicle come into the capsule of the organ through that minute hole.

In order that this minute hole and its relation to other parts may be more fully studied, we have prepared Plate iii., which is a large drawing representing the Wolffian body D with the young kidney K, and the sliced capsule of the young testicle H, in which the letter B points to the hole in the capsule as seen from its inside.

The Müllerian duct C is well seen, and folds of peritoneum A pass up from the end of the Müllerian duct and Wolffian body towards the diaphragm of the young animal. A large part of the capsule of the testicle has been sliced away in order to show the hollow in which the testicle lies between the lower part of the kidney K and the upper part of the Wolffian body D.

Stretching down from the lower part of the testicle H is a strong band of a fibrous nature G, the gubernaculum testis, which passes down in continuity with the peritoneal layer which spreads over the lower end of the Wolffian body and the string F formed by the junction of the Müllerian and Wolffian ducts at their lower ends. This drawing has been most faithfully drawn by means of a binocular microscope, and is true to nature; but to understand it the more clearly, we must now look at Fig. 3 Plate ii. which represents the appearances seen in a fœtal deer considerably younger than figure 4 represents.

In Fig. 3 we have faithfully represented the two kidneys K K, the two testicles B B, and the two Wolffian bodies D D, as seen by means of a binocular microscope on looking into the body of a fœtal deer, less than two inches in length, prepared by a most careful dissection to show all such parts in their natural positions. I shall not refer to the other structures repre-

sented in the meantime, but the proper description of this important drawing will be found attached to the plate. What I wish particularly to direct attention to is the stalked condition of the young testicles B B, at this stage of their development. The letters X X point to the stalks by which the testicles are attached to the Wolffian bodies at their upper part. These stalks of connection are seen in all young testicles at this age; and on looking at Fig. 4 again, which, as already mentioned, is drawn from the appearances seen in the body of a fœtal deer somewhat older, it will be noticed that the stalks are not visible, the reason being that here the testicles are much larger and more globular, and thus hide from view the stalks of connection through the centre of which pass certain structures. In the case of the younger animal as seen in Fig. 3, the testicles are more elongated and less globular, and thus their stalks of connection, X X, with the upper end of the Wolffian bodies are not only well marked but are well seen. I would here like to remark that this entire drawing has been made with the greatest care and attention to all points, and it very faithfully represents the parts described.

Having thus, by means of these figures, directed attention to the stalk of the peritoneum which connects the young testicle with the upper part of the Wolffian body, and to the minute holes seen within the capsules of the testicle always at the same spot, which undoubtedly give passage to some structures passing from the Wolffian bodies into the capsules of the testicles, let us now in the next place try to find the exact position of the Wolffian duct and its relation to the testicle and Wolffian body.

Where is the Wolffian duct to be found? A part of the Wolffian duct can always be found at the lower end of the Wolffian body, where in conjunction with the pelvic end of the Müllerian duct, it passes down to become attached to the cloaca. The two Müllerian ducts as they course downwards along the outer borders of the Wolffian bodies, at last meet each other in the middle line in the pelvic region. In the female this junction of the lower ends of the Müllerian ducts results in the formation of the body of the uterus, and the Müllerian ducts in the upper parts become the Fallopian tubes. The two Wolffian ducts join the two Müllerian ducts as they pass down behind the allantoic stalk and the four ducts

together form the genital cord, or string, which passes down to be connected with the sinus urogenitalis at the base of the allantoic stalk. But it is at its upper part that the Wolffian duct is so difficult to find. That part of the Wolffian duct which becomes the epididymis and the vas deferens is very difficult to discover. After long seaching I discovered the upper part of the Wolffian duct in the following way. See Plate i. Fig. 1. Here is represented the Wolffian body D, with the kidney K and the testicle B and the Müllerian duct C, and the gubernaculum testis G. On the right side the Wolffian body has been cut in half and its exposed cut surface M is seen. At the lower part of the same figure the letter E points to a string formed by the Müllerian duct in front and the Wolffian duct behind. These two ducts join the same ducts coming down from the right Wolffian body at H, and form the genital cord or string. The letter N here points to a torn surface, a point at which the allantoic stalk was attached to the genital cord, and at L can be seen a structure which is evidently the verum montanum prominence, and supposed to be the homologue of the hymen in the female. Now if the right Wolffian body is thus cut in half and the genital cord thus torn away from the allantoic stalk, the left Wolffian body with the testicle attached to it may be then lifted up and turned right over on to its side.

If this is properly done, then we bring into view the appearances seen in Fig. 2, which represents the left Wolffian body lying on its side in such a way as to expose the torn mesorchium E E and the under surface of the left testicle B, and the gubernaculum testis G is well brought into view; under low powers of the microscope a tubular structure H H can now be seen passing upwards from under cover of the upper border of the mesorchium towards the testicle with which it comes into intimate relation at the spot indicated by the letter H. The letter L points to a small cyst which springs from the Wolffian duct before it reaches the testicle. The Wolffian duct thus exposed lies under the peritoneum covering the Wolffian body, and its own fibrous covering is in direct continuity with the peritoneal and fibrous capsule of the testicle. We must be careful not to mistake the gubernaculum testis for the Wolffian duct—between which there is no connection; but on looking down into the body of a young fœtal deer, this gubernaculum

testis as it leaves the lower end of the testicle covers both the Wolffian duct and Müllerian ducts at their pelvic ends, and may possibly be mistaken for the Wolffian duct. The Wolffian duct in its upper part cannot be seen except by turning over on to its side the whole Wolffian body with the testicle attached. There it is at once seen as in Fig. 2 as a rod-like structure H H quite apart from the gubernaculum testis G.

In Fig 1, the gubernaculum testis G is well seen, but the Wolffian duct cannot be seen in this front view of the Wolffian body and testis.

How does the Wolffian duct become attached to the testicle at its upper part?

The Wolffian duct is at its upper part firmly connected with the capsule of the testicle—see Plate iv. Fig. 6—which represents the capsule of the testicle firmly attached by the peritoneal stalk to the upper part of the Wolffian body. The letter B points to the hole in the capsule which passes through the centre of the stalk. Fig. 7 represents the Wolffian duct C attached to the capsule of the testicle B. The Wolffian body is lying on its side with its under surface exposed to show the Wolffian duct C. The fibrous capsule of the testicle is continuous with the fibrous covering of the Wolffian duct. Fig. 8 shows the capsule of the testicle B partly torn away from the stalk of peritoneum H. The Wolffian duct still atached to the capsule of the testicle is also partly torn away from the Wolffian body as seen at the letter M. In Fig. 9, we see in the clearest manner that when the capsule B of the testicle is partly torn away from the stalk H, the Wolffian duct goes with it, and that the Wolffian duct is actually torn away from the Wolffian body as is seen in the torn surface M. And just at the spot on the capsule where it joins the stalk from the Wolffian body there can be seen a scar L indicating a torn surface; the capsule of the testicle has been torn through at this point. The study of the Figs. 8 and 9 leads us to the conclusion that the capsule of the testicle and the covering of Wolffian duct are continuous with each other, just as the bowl of an ordinary clay pipe is continuous with its stem.

Much has been said about the stalk which connects the capsule of the testicle with the Wolffian body at its upper part. It is only at a certain stage of development that this stalk can be so well seen, as is shown at X in Fig. 3 Plate ii. Although

it is always present at a certain stage, and can always be seen before the testicle has enlarged and become globular, it is gradually hidden from view behind the enlarging testicle, and so may be overlooked ; but it is always present as an essential part in the development of the testicle.

We must now go to the microscope to tell us the nature of this stalk, and the nature of those structures which pass through its centre into the capsule of the testicle. It is possible to make serial sections through the testicle and Wolffian body in various directions as they are naturally and firmly attached to each other by that stalk ; and fortunately I have succeeded in making such sections which pass vertically downwards through both testicle and Wolffian body and through the stalk which connects them, and also transverse sections, in series, through the Wolffian body and testis at the same part.

The first thing that is noticed in viewing such a vertical section is the strong fibrous capsule of the young testicle (see Figs. 10 and 11, Plate v.). The letter A points to this strong capsule in each figure. Nothing of the kind exists in the sections of an ovary at this same stage of development ; and on looking carefully at Fig. 10 it will be seen that the whole tubular structure of the testis B is enclosed within the fibrous capsule, and that it has no outlet from the organ except by a minute aperture which passes through the centre of the stalk X, so often referred to. In Plate ii. Fig. 4, these minute apertures in the capsules of the testicles are well seen at the spots indicated by the letters B B. In Fig. 10 Plate v., which is now before us, the microscope has shown to us that in nature this minute aperture is occupied by a complex cellular column (see X, Fig. 10), which passes through the stalk centre. This solid cellular column X can be seen coming up from the Wolffian body and passing through the centre of the peritoneal stalk right into the capsule of the testicle, and as soon as it is well within the capsule of the testicle it gives out branches of cells in all directions as it grows forward in the long central axis of the testicle. It grows so far forward that it almost comes in contact with the enclosing capsule at the extreme end of the gland ; cellular branches spring out in all directions from it, until the testicle capsule is tightly distended with these rudimentary tubuli seminiferi. I have described the central column of cells which passes from the Wolffian body into the

testicle as a solid cellular column. Under very high powers of the microscope it is possible to see in the substance of this cellular column appearances which can only be described as transverse sections of minute tubules. The branches of cells which radiate in all directions from this central cellular column butt up closely against the capsule of the testicle, and on careful examination under high powers of the microscope numerous transverse sections of minute tubes can be seen in all directions, and it is quite evident that all these cellular offshoots from the central column have become minute tubules and are all in direct communication with the solid column of cells from which they have outgrown. Each small tube consists of a basement membrane on which is a single layer of more or less columnar nucleated cells. All these tubes are blind at their ends as far as can be seen, and the epithelial cells lining these numerous tubes are without doubt derived from the central cellular column. The central cellular column as it passes into the testicle is surrounded on all sides by a thick coating of peritoneum which constitutes the stalk, and this stalk can be seen to give rise to the whole capsule of the testicle, which is now distended with the tubules which have sprung out in all directions from the cellular column X. On tracing the central cellular column back from the testicle towards the Wolffian body we find it goes back through the centre of the stalk until it ends in the immediate neighbourhood of a number of cut tubules, as indicated by the letters H H H in Fig. 10, and this neighbourhood is the very spot towards which we have traced the end of the Wolffian duct; and there can be no doubt that the cut tubules as represented by the letters H H H in Fig. 10, and by the same letters in the transverse section, Fig. 11, are the cut tubules of the Wolffian duct with which the cellular column is in direct continuity. All these parts are, of course, seen in transverse section; but an examination of a whole series of such preparations, both vertical and transverse, shows that the convoluted terminal end of the Wolffian duct is in direct continuity with that central cellular column X, which enters the testicle through the centre of the peritoneal stalk, and which, as soon as it is within the capsule, gives out branches of tubules in all directions until the capsule itself becomes globular from such distention.

The Wolffian duct in its whole course from the testicle to

its pelvic end is in connection with the tubules of the Wolffian body. It receives branches of tubes from the Wolffian body along its course, especially at its lower end; and at its upper end it receives, either directly or indirectly, the whole tubular structure of the testicle by means of the cellular column which passes through the peritoneal stalk from the capsule. In all probability this central cellular column X gives rise later on to the vasa efferentia, which are in direct continuity with the convoluted tubules of the epididymis.

In Fig. 11, which is a transverse section of the young testicle, the central tubular column X is well seen giving out its tubules in all directions, and the letters H H H point to cut tubes with which the column X is undoubtedly continuous. As these figures, 10 and 11, are carefully drawn from microphotographs, their accuracy may be relied on.

Let us now, in conclusion, follow the steps in the development of the testicle from the first appearance of the gland at the upper and inner part of the Wolffian body.

The Wolffian body in the early embryo has already been described, and in Plate vii. Fig. 15 this is again represented in order that the primitive germinal ridge G may be seen at its upper part B swelling out, and fading off into the substance of the Wolffian body. It is at this point that the young testicle makes its first appearance as an outgrowth from the Wolffian body. In Plate vi. Fig. 14 shows in transverse section through the body of a young embryo the Wolffian bodies and the first trace of the genital gland, to which the letters B B point. On comparing this young gland with Fig. 13 or with Fig. 15, it is quite clear that the young gland is an outgrowth of vascural stroma from the Wolffian body, capped by a thick layer of epithelial cells. The whole primitive germinal ridge may be looked upon as a thick fold of peritoneum projecting from the inner aspect of the Wolffian body; but at its upper end certain structures grow into its substance from the Wolffian body, and in that situation the epithelial cells covering this germinal ridge become thickened as a layer over that part. The next step in the development of the testicle is the distinct bulging forward of the young gland as an elongated body having a stalk-like connection with the Wolffian body. In Fig. 16, Plate vii., we have a faithful representation of the young testicle as it thus appears. Microscopic sections of such a young

testicle show that its stalk X consists of thickened peritoneum, and that through the centre of the stalk passes a solid-like column of cells, from which spring out in all directions minute tubules, the future tubuli seminiferi of the adult testicle, and all these tubules are enclosed within a fibrous capsule of peritoneum continuous with the thick stalk itself. Here, then, we have clear evidence that the young testicle is a sub-peritoneal outgrowth from the primitive germinal ridge, pushed out, as it were, into the form of an elongated body by certain continually growing tubules which pass into its base from the Wolffian body through the centre of a stalk-like connection of peritoneum. I speak of it as a sub-peritoneal outgrowth, because sections show that the essential tubular structure is sub-peritoneal from the first. The capsule of the testicle is formed out of the primitive germinal ridge, which is itself at first a thickened fold of peritoneum on the inner aspect of the Wolffian body, as already described. It is now very interesting to follow the next step. As the testicle continues to grow and enlarge, it drags forward with it that part of the primitive germinal ridge which is immediately below it, and with which it is continuous; for it must be borne in mind that the capsule of the testicle and the rest of the germinal ridge are peritoneal structures, and both parts of the primitive germinal streak, so well seen in the early embryo. That part of the germinal ridge immediately below the capsule of the growing testicle becomes the gubernaculum testis G, and, as a fold of peritoneum, it passes down and fades off into the general peritoneal layer which covers the pelvic organs and lines the general cavity of the pelvis later on.

As the testicle thus becomes larger and more globular, its stalk-like connection with the Wolffian body becomes hidden from view. The stalk becomes much shorter and almost disappears as the capsule is distended outwards in a centrifugal manner by the continued growth of the tubuli seminiferi within it. In the figure, 17, the stalk cannot be seen though a fold of peritoneum is seen passing upwards off the surface of the testicle to become continuous with the peritoneum covering the body cavity of the embryo.

To establish the position of the Wolffian duct and its relation with the testicle at the very early stages of development is most important, bearing in mind that it is this duct, as the

vas deferens, which carries off the secretion of the tubuli seminiferi.

Looking down on the upper surface of the testicle and Wolffian body, as in Fig. 17, the Wolffian duct cannot be seen, but on raising up the Wolffian body and turning it over on to its side, as in Fig. 18, the Wolffian duct H H is clearly brought into view, and it always holds this position as regards the Wolffian body and the testicle; and, lastly, it is quite evident on looking at Fig. 10, Plate v., that the tubuli seminiferi are all in direct connection with, and derived from the cellular column X, which passes through the stalk to be connected with the Wolffian duct.

That the central solid column X, which passes through the stalk into the capsule of the testicle, gives rise to the tubuli seminiferi cannot be doubted. It is for further researches to settle the question as to whether both the Müllerian and Wolffian ducts are of epiblastic origin. In several of my microscopic sections there is distinct evidence of a communication between the Müllerian ducts and the tubules of the Wolffian body which join the Wolffian duct itself.

In conclusion, while it is quite clear that the germinal vesicles of the ova are derived from germ epithelial cells, it has not yet been proved that either the cells lining the Graafian follicles or the cells lining the tubuli seminiferi have their origin from germ epithelial cells. But if it can be shown that the Wolffian ducts have an epiblastic origin, then both the tubules of the testicle and the cells lining them can be satisfactorily accounted for. If the tubules of the testicle, as I have attempted to show, are derived from the terminal end of the Wolffian duct, then it is most probable that the epithelial cells lining those tubules have the same origin as the tubules themselves. In other words, according to these observations, if the Wolffian ducts and the tubuli seminiferi are of epiblastic origin, then the cells lining the tubuli seminiferi are also of epiblastic origin.

Description of Figures.

PLATE I.

Fig. 1.—To show relation of Wolffian Body to Testis and Kidney.

A Blind end of Müllerian Duct.
B Testicle.
C Müllerian Duct.
D Wolffian Body.
E String formed by Müllerian and Wolffian Ducts.
G Gubernaculum Testis.
H Junction of Müllerian Ducts in middle line.
K Kidney.
L Structure, supposed to be the Verum Montanum.
M Cut surface of Right Wolffian Body.
N Torn surface remaining after the allantoic stalk is removed.

Fig. 2.—The Wolffian Body lying on its side to show the Wolffian Duct passing upwards to Testicle.

A Fold of Peritoneum from Wolffian Body and Testicle passing upwards towards diaphragm.
B Testicle.
D Wolffian Body.
E E Torn edge of the Mesorchium.
F Wolffian and Müllerian Ducts.
G Gubernaculum Testis.
H H Wolffian Duct.
L Small cyst attached to Wolffian Duct.

PLATE II.

Fig. 3.—The Wolffian Bodies as seen in a fœtal Deer about 2 inches in length.

A Fold of Peritoneum passing from upper end of Wolffian Bodies to the diaphragm.
B Testis.
C Müllerian Ducts.
D Wolffian Bodies.
E Wolffian and Müllerian Ducts in contact.
F Umbilical Artery.
K Kidney.
M Allantoic stalk.
R Rectum.
N Stalk of Peritoneum connecting Testicle with Wolffian Body.

Fig. 4.—To show the minute holes in the Capsules of Testicles through which certain tubular structures pass.

A Fold of Peritoneum from Wolffian Body.
B Hole in Capsule of Testicle.
C Müllerian Ducts.
D Wolffian Body.
G Gubernaculum Testis.
K Kidney.
M Umbilical Artery.
N Allantoic stalk.
R Rectum.

PLATE III.

Fig. 5.—Highly magnified view of Wolffian Body to show the hole in the Capsule of Testicle through which certain tubular structures pass.

A Folds of Peritoneum passing upwards.
B Hole in Capsule of Testicle.
C Müllerian Duct.
F Müllerian Duct and Wolffian Duct.
G Gubernaculum Testis.
H Capsule of Testicle, sliced away in part.
K Kidney.

PLATE IV.

Fig. 6.—Wolffian Body with Capsule of Testicle attached to show the hole B in Capsule.

A Peritoneal Fold passing upwards.
B Capsule of Testicle with hole seen at upper part.
C Müllerian Duct.
D Wolffian Body.
G Gubernaculum Testis.

Fig. 7.—Under surface of Wolffian Body to show Wolffian Duct.

B Capsule of Testicle.
C Wolffian Duct joining Capsule of Testicle.
D Wolffian Body.
E Cut edge of Mesorchium.
F Müllerian and Wolffian Ducts.
G Gubernaculum Testis.

Fig. 8.—To show Capsule of Testicle with Wolffian Duct, partly torn away from Wolffian Body.

B Capsule of Testicle with hole in it.
C Müllerian Duct.
D Wolffian Body.
G Gubernaculum Testis.
H Stalk from which Capsule of Testicle is torn away.
M Torn surface on Wolffian Body—the site of the Wolffian Duct, now torn away.

FIG. 9.—Under surface of Wolffian Body to show Capsule of Testicle with Wolffian Duct torn away from stalk and from Wolffian Body.

B Capsule of Testicle.
C Müllerian Duct.
D Wolffian Body.
H Stalk of Peritoneum from which Capsule of Testicle is torn.
L Torn surface of Capsule of Testicle.
M Site of Wolffian Duct, now torn away from Wolffian Body, along with Capsule of Testicle.

PLATE V.

FIG. 10.—Vertical section through Wolffian Body and Testis to show origin of Tubuli Seminiferi.

A Fibrous Capsule of Testicle continuous with peritoneal stalk.
B Central cellular column from which proceed all the Tubuli Seminiferi.
F Glomeruli in Wolffian Body.
G Gubernaculum Testis.
H H H Cut tubules from Wolffian Duct.
N Cellular column passing into Capsule of Testicle to give origin to the Tubuli Seminiferi. This column passes through the centre of the peritoneal stalk.

FIG. 11.—Transverse section of Testicle and Wolffian Body.

A Fibrous Capsules of Testicle.
B Tubuli Seminiferi.
H H H Cut Tubules of Wolffian Duct.
N Transverse section of central cellular column from which arise the Tubuli Seminiferi, in the centre of Testicle.

PLATE VI.

FIG. 12.—The Body of an embryo Deer less than one inch in length to show the Wolffian Bodies with the primitive germinal streaks.

B Wolffian Body at upper end.
C Müllerian Duct.
D Wolffian Body.
E Primitive germinal streak.
G Cut mesentery in middle line.
H Head of Embryo.
L Anterior limb.
N Tail.
P Posterior limb.

FIG. 13.—More highly magnified view of one Wolffian Body from this embryo Deer, to show primitive germinal ridge or streak, at its upper part fading off into the Wolffian Body.

B Upper part of Wolffian Body with germinal ridge.
C Müllerian Duct.
D Wolffian Body.
E Germinal ridge or streak.

FIG. 14.—Microphotograph—Transverse section through body of this embryo Deer, to show the Wolffian Bodies in section and the young genital glands.

A Neural canal.
B Young genital gland—Ovary or Testis.
C Müllerian Duct in section.
D Tubules in Wolffian Body.
E Glomeruli with branches from Aorta.
F Chorda Dorsalis.
G Central Mesentery.
M Aorta full of blood corpuscles.

PLATE VII.

FIG. 15.—The four figures on this plate are to show the different steps in the development of the Testicle.

B The germinal ridge or streak fading off into the Wolffian Body. It is at this spot that the Testicle first appears.
C Müllerian Duct.
D Wolffian Body.
G Primitive germinal ridge or streak.

FIG. 16.—A stage in the development of the Testicle which now appears as an elongated body connected with the Wolffian Body by means of a thick peritoneal stalk.

B Testis.
C Müllerian Duct.
D Wolffian Body.
F Müllerian and Wolffian Ducts.
G Gubernaculum Testis.
N Stalk from the Wolffian Body connected with the out-growing Testicle.

FIG. 17.—A further stage in the development of the Testicle, the stalk is now hidden from view by the larger and more globular Testicle.

B Testicle.
C Müllerian Duct.
D Wolffian Body.
E Müllerian and Wolffian Ducts.
G Gubernaculum Testis—the remains of the germinal ridge.

FIG. 18.—Under surface of Wolffian Body to show Wolffian Duct in its relation to the Testicle.

B Testicle.
E E Cut Mesorchium.
H H Wolffian Duct—The Capsule of Testicle is continuous with the covering of the Wolffian Duct.
G Gubernaculum Testis,—which in the female is known as the round ligament of the ovary.

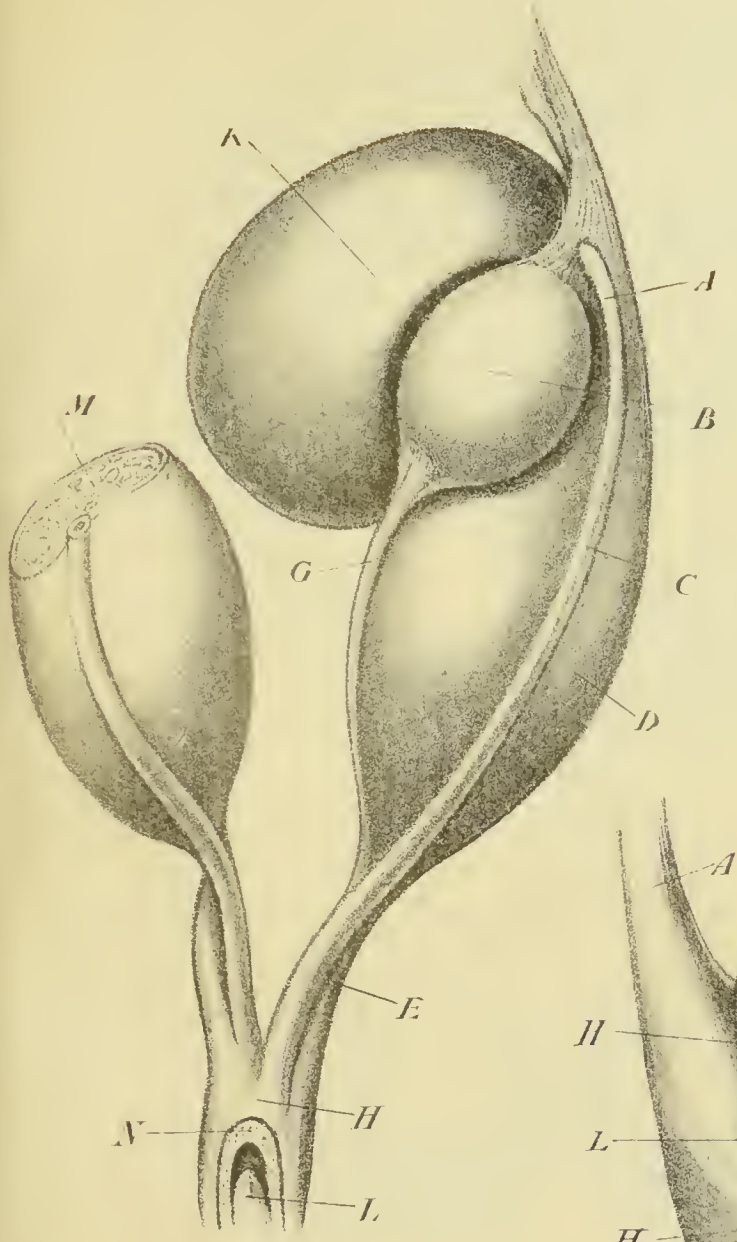


Fig. 1

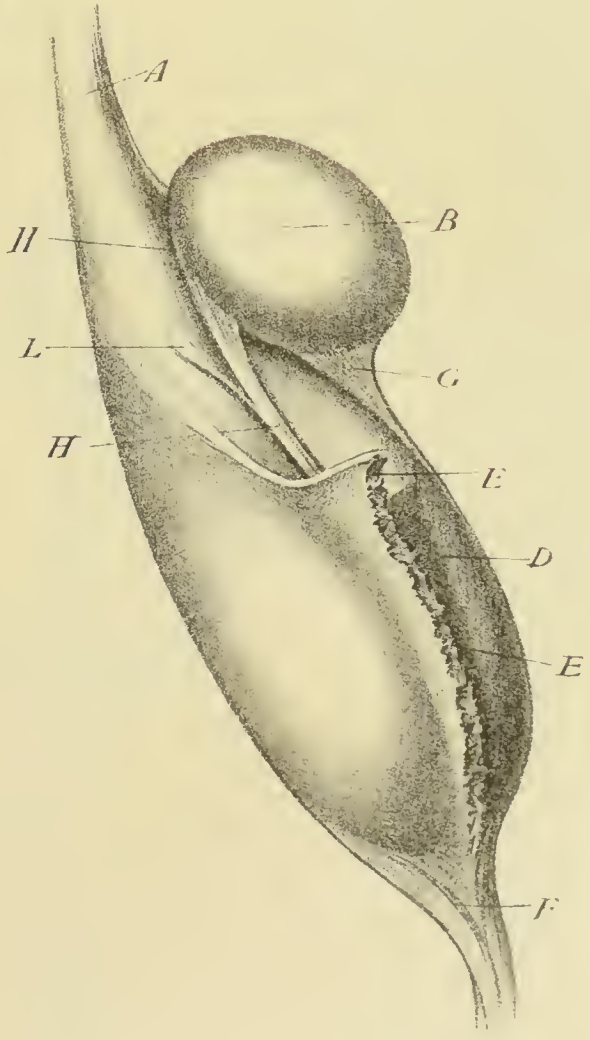
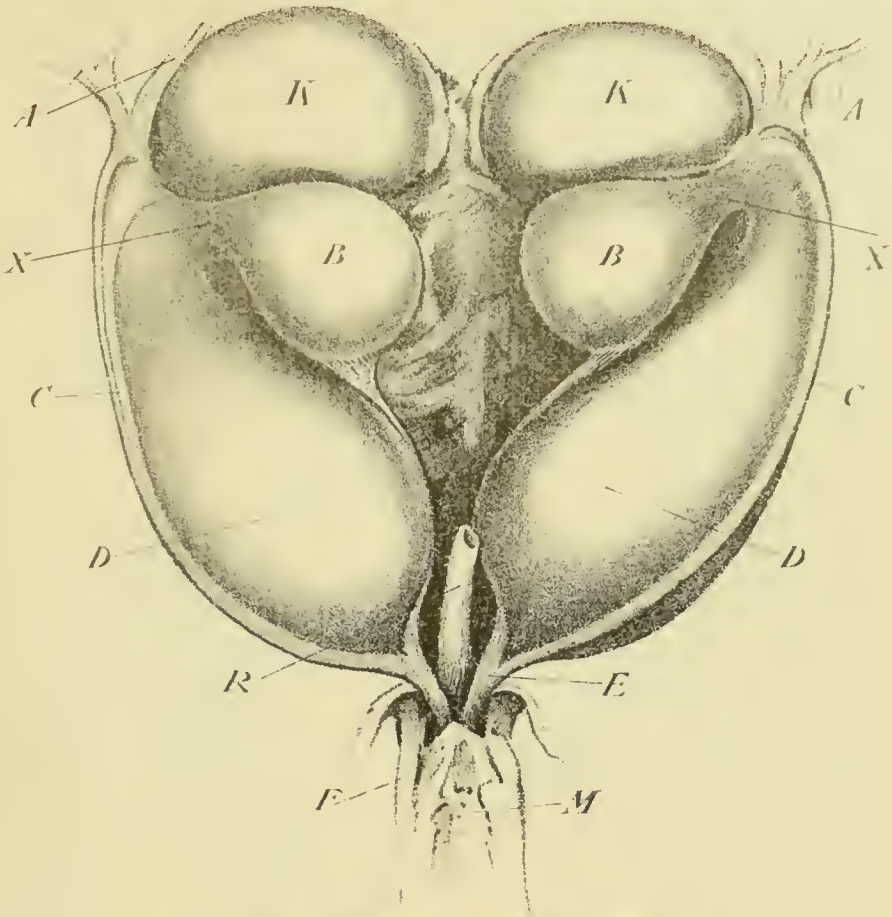


Fig. 2

Fig. 3



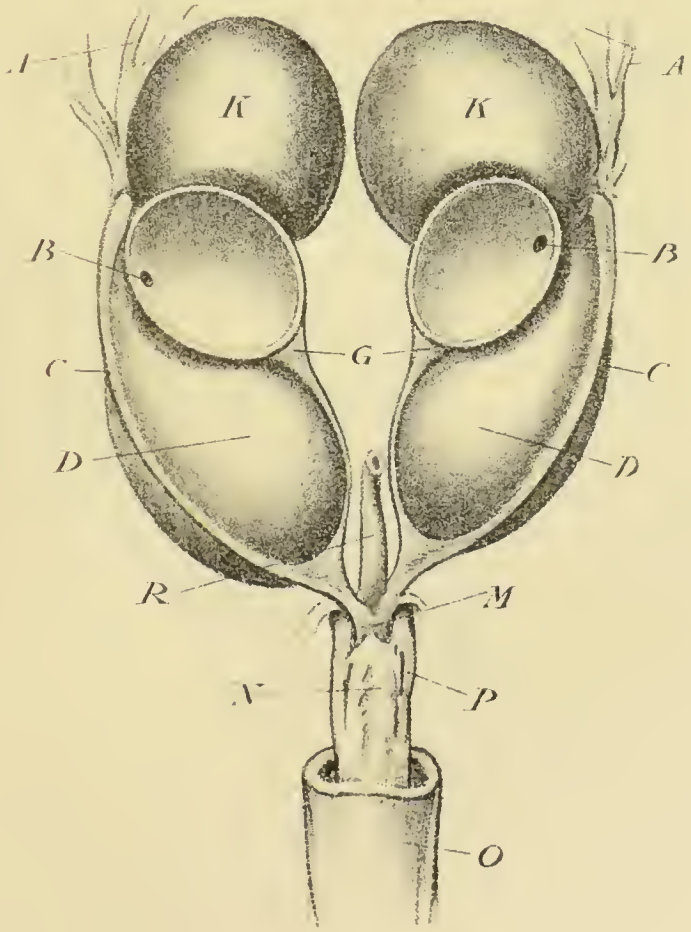


Fig. 4

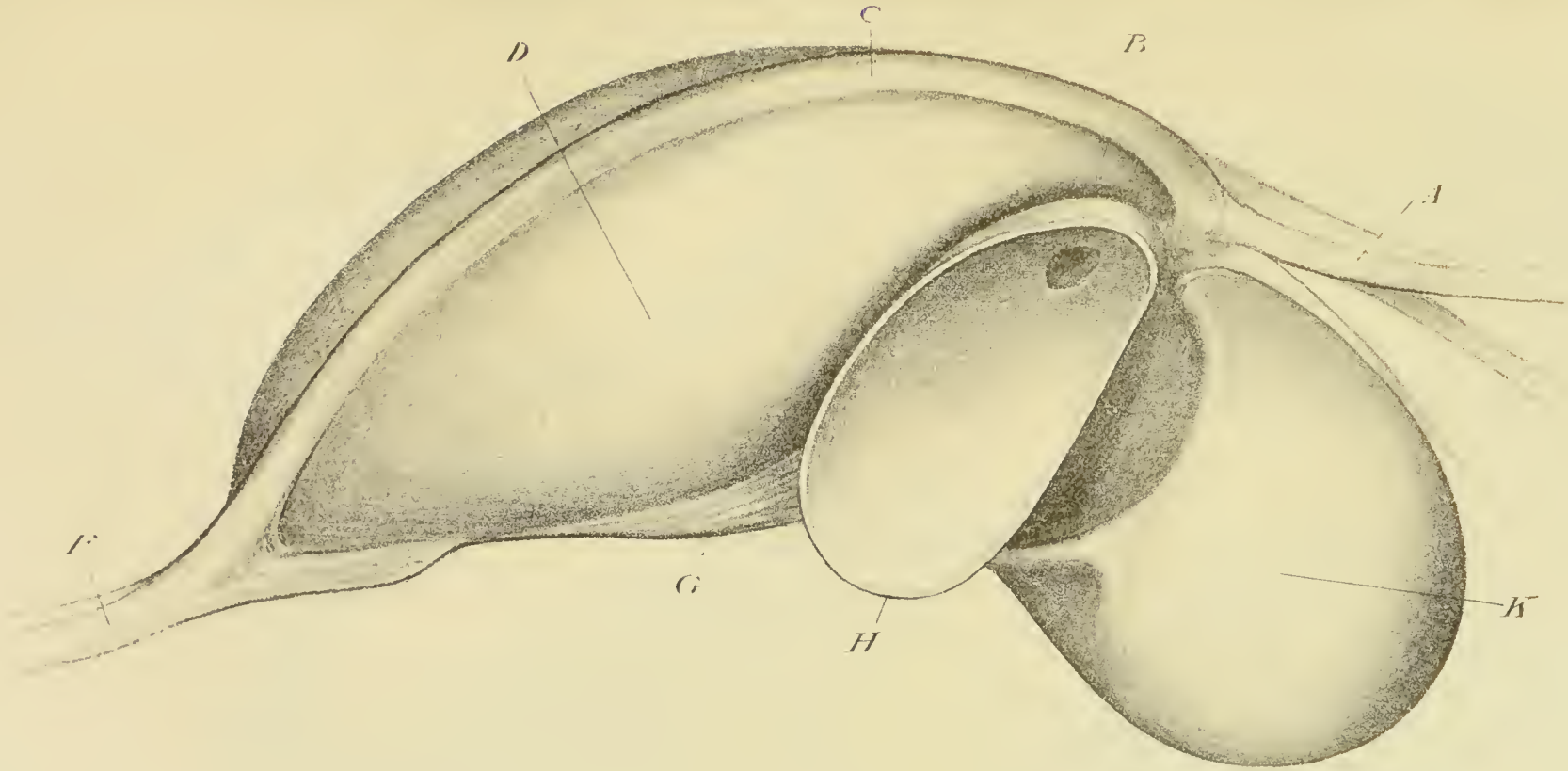
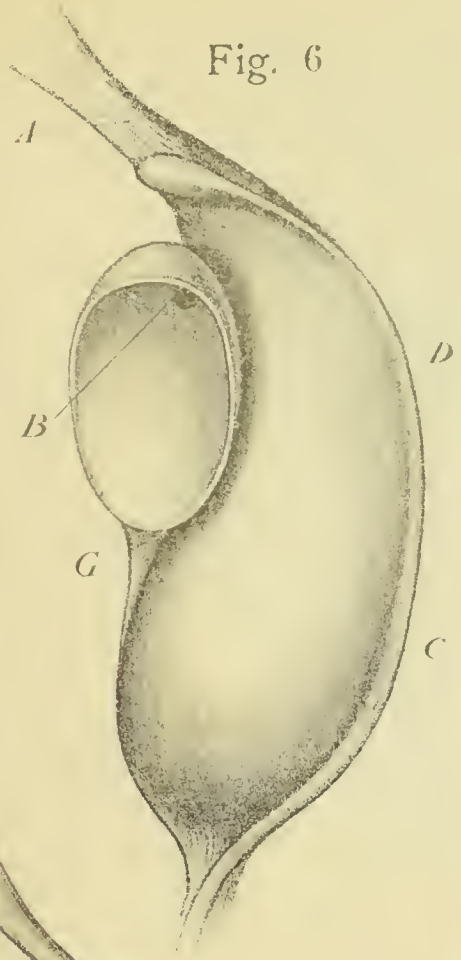


Fig. 5

Fig. 6



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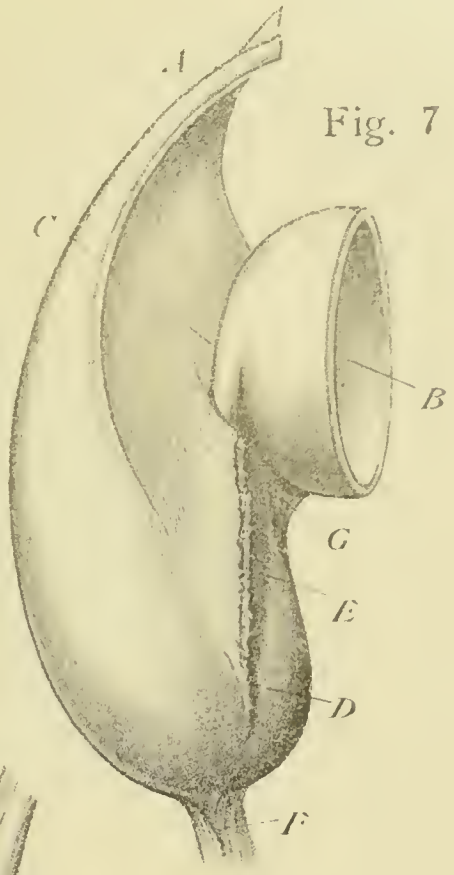


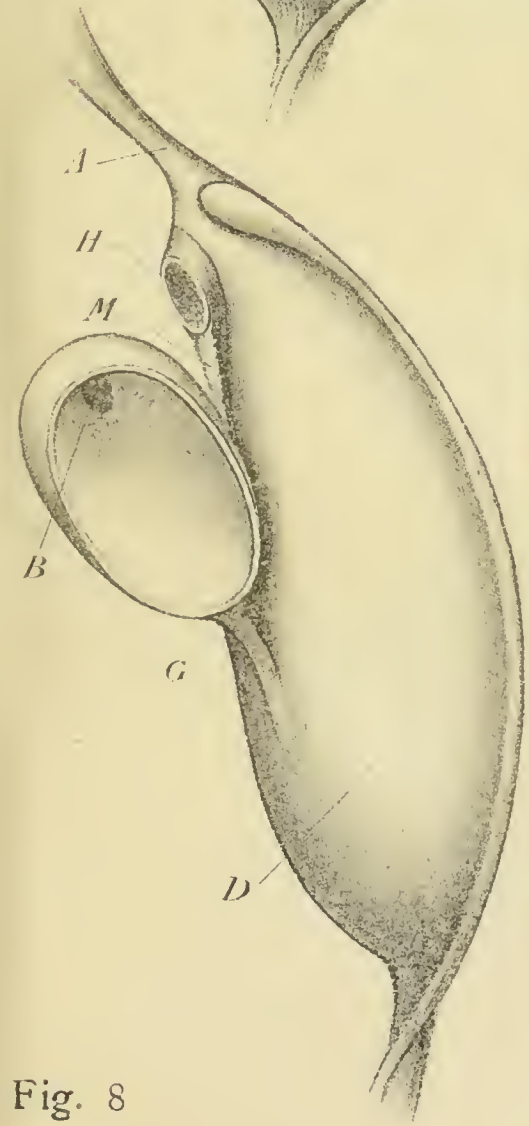


Fig. 8

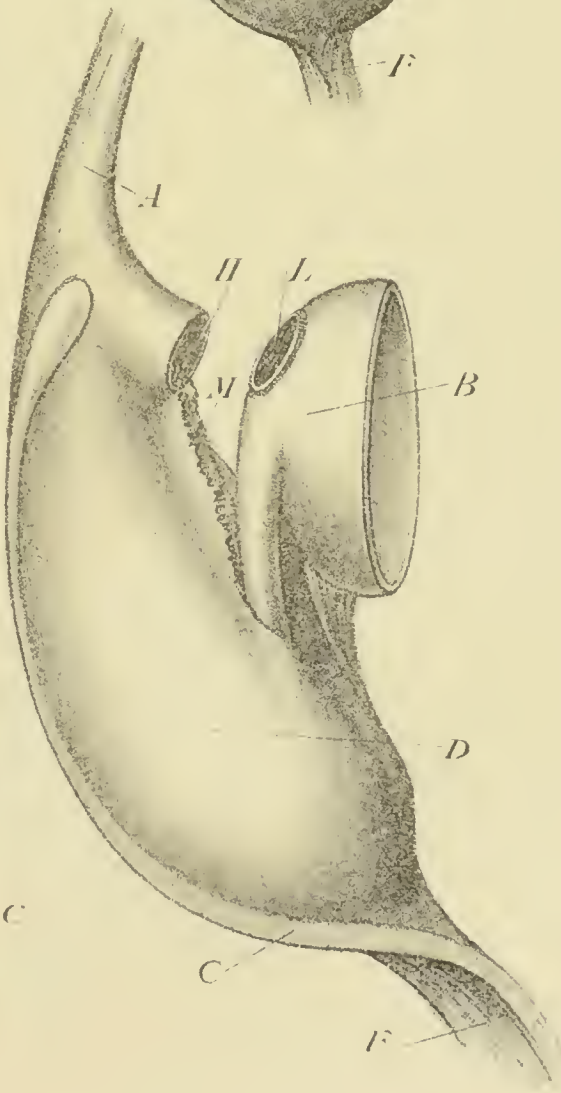


Fig. 9

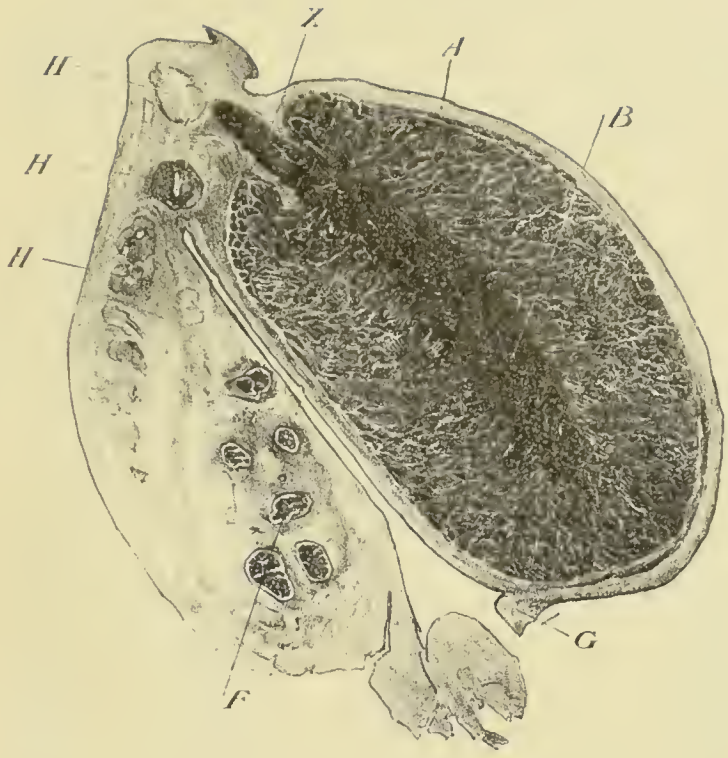


Fig. 10

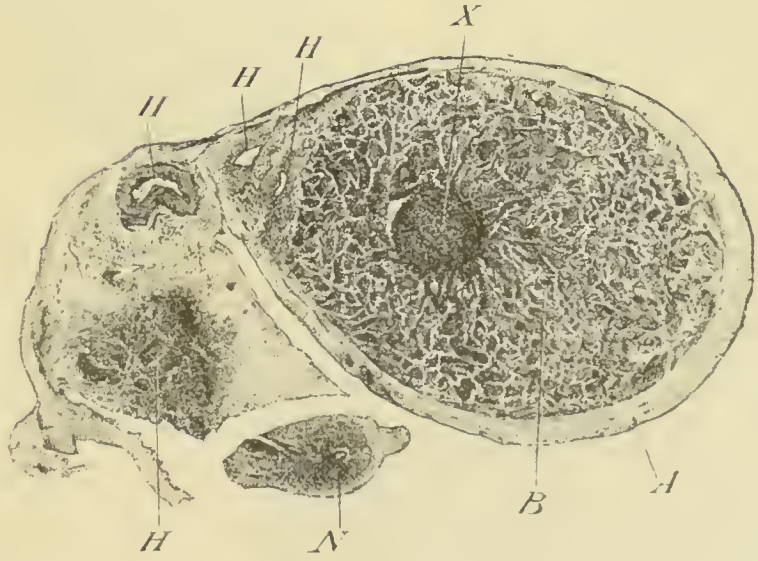


Fig. 11

Fig. 12

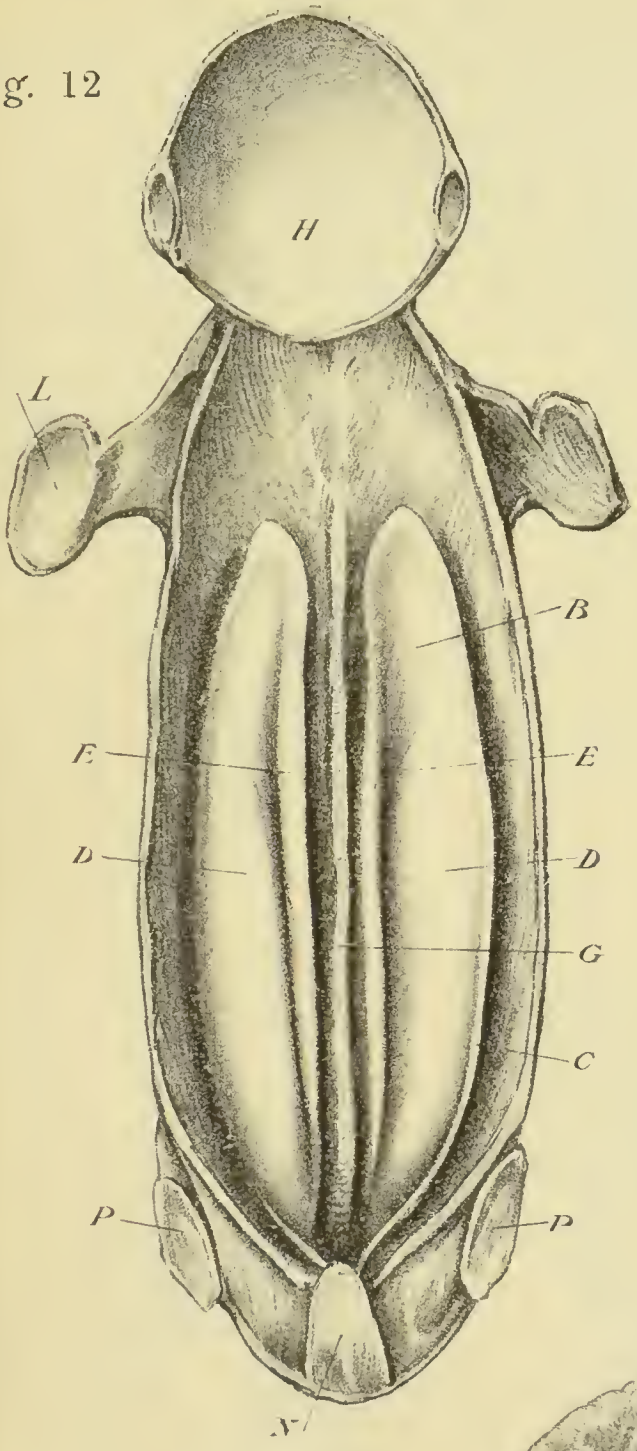


Fig. 13

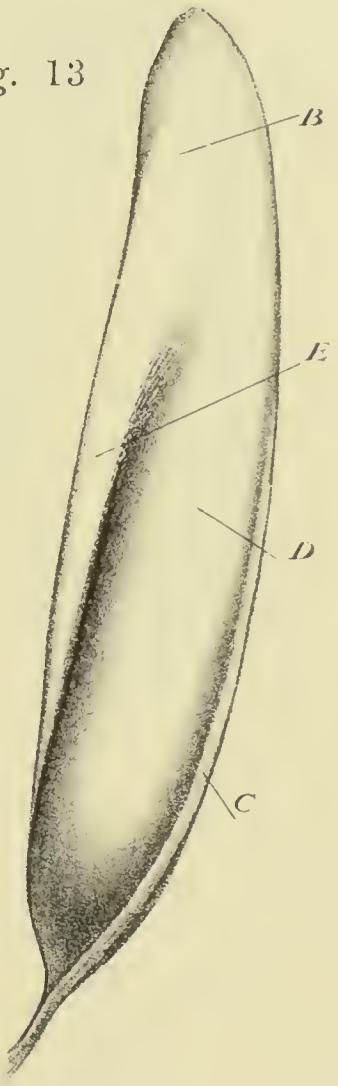


Fig. 14

Fig. 15

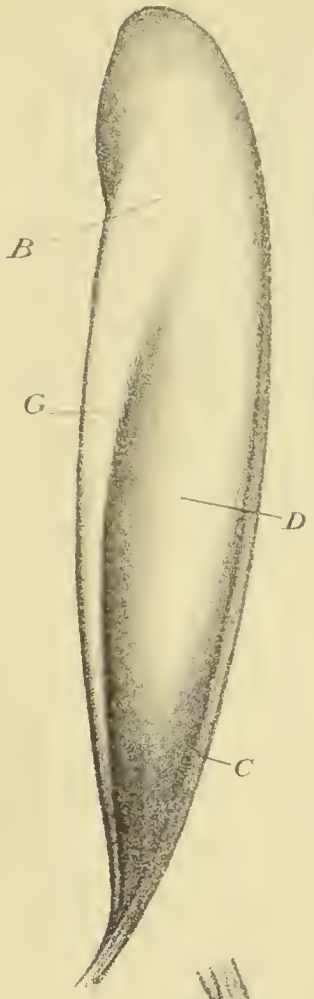
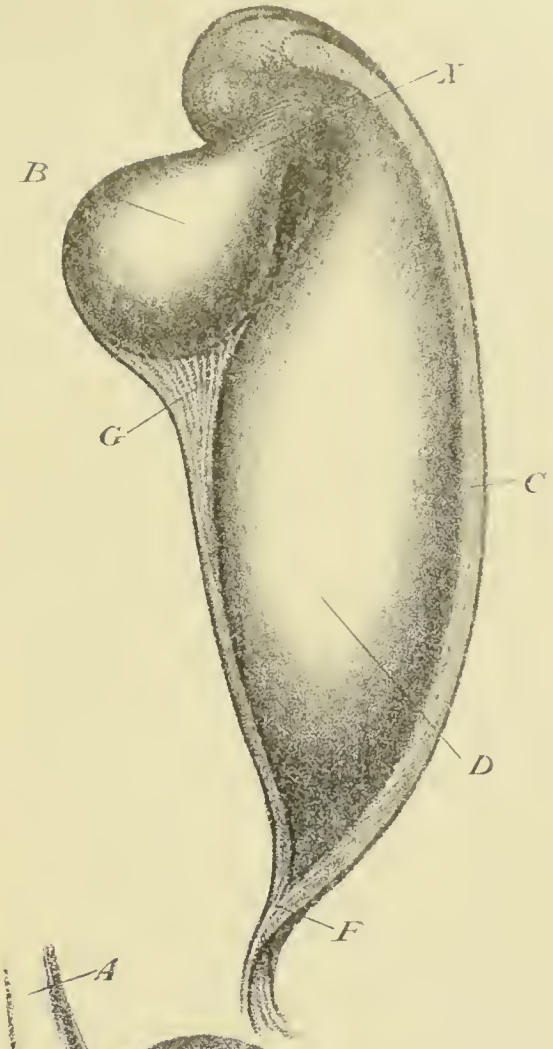


Fig. 16



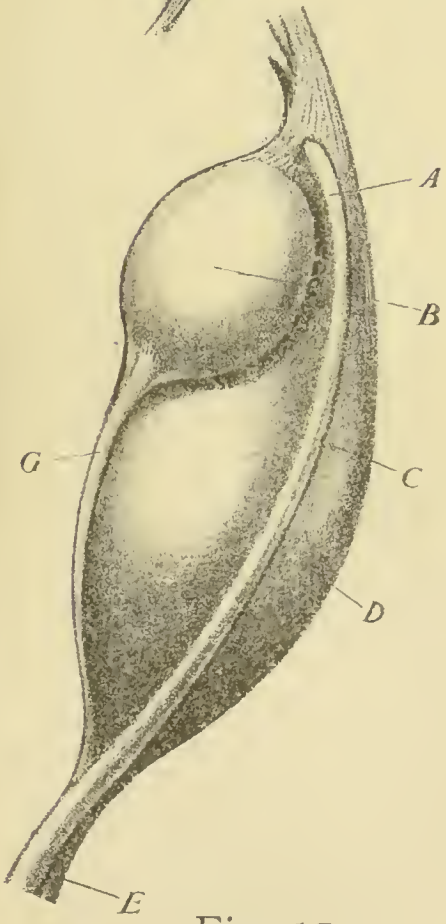


Fig. 17

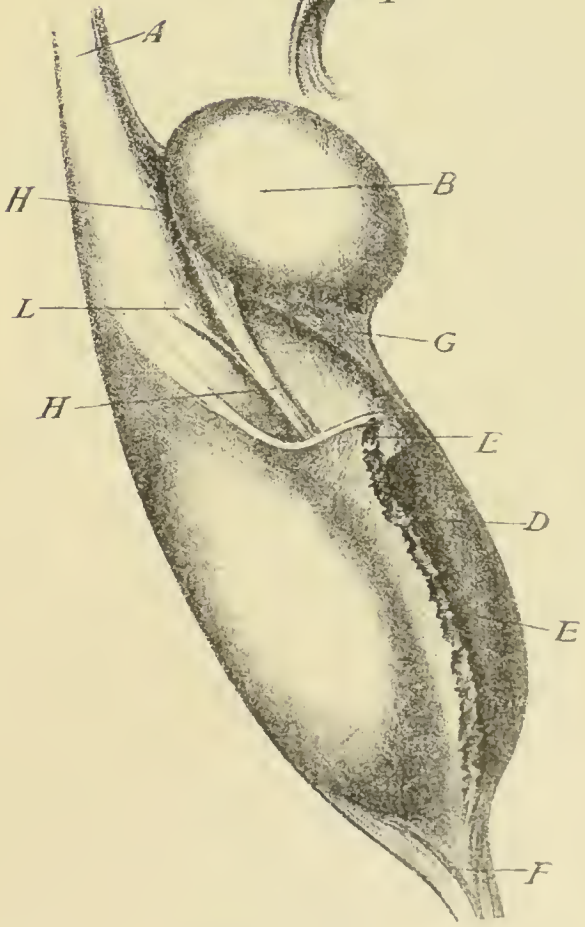


Fig. 18